

Does hydraulic lift or nighttime transpiration facilitate nitrogen acquisition?

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Abstract Water movement from roots to soil at night in the process of hydraulic lift (redistribution) rehydrates the rhizosphere and has been proposed to improve plant nutrient acquisition. Another process that has now been found in many plant species is nighttime transpiration and this could also affect nutrient relations by influencing supply of mobile nutrients to roots at night. The effects of these soil/root water relations interactions have not been adequately tested. We chose ten *Sarcobatus vermiculatus* (Hook.) Torrey shrubs with different magni-

tudes of hydraulic lift (i.e. diel range in soil water potential) to test the hypothesis that the magnitude of lift would be positively related to the amount of nitrogen (N) uptake over a period of days. A ^{15}N tracer was injected in the 20–30 cm soil layer at locations with hydraulic lift to determine plant ^{15}N acquisition by shallow roots conducting hydraulic lift. Half of the plants were also placed in large humidified tents (i.e. “bagged”), which suppressed nighttime transpiration, and thus were expected to have greater magnitudes of hydraulic lift, although they did not. All plants took up the ^{15}N tracer, but contrary to our hypothesis the magnitude of hydraulic lift had no significant effect on the amount of ^{15}N acquired over a 9-day period following labeling. However, plants that were bagged tended to have lower ^{15}N acquisition ($P=0.07$). These data indicate that decreased nighttime transpirational water loss or some other effect of bagging may decrease nutrient acquisition by these nutrient-limited phreatophytic shrubs and more generally suggests a possible nutritional benefit of nighttime transpiration by plants. This suggestion needs more thorough testing to elucidate an important potential link between plant water and nutrient relations.

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Introduction

Plant water use behavior includes some unexpected patterns of water movement between roots and soil as well as timing of water use. Hydraulic redistribution and nighttime transpiration are processes now documented in many species (Caldwell et al. 1998; Caird et al. 2007). These processes have been found to co-occur in plants, including in some cold-desert shrub (Donovan et al. 2003) and neotropical tree (Domec et al. 2006) species. Moreover, both processes affect root–soil water transfer at night and have been hypothesized to affect nutrient acquisition, independently or interactively, but these hypotheses have not been tested.

Hydraulic redistribution is a process whereby plants passively redistribute water through their root systems from wetter to drier soil locations along existing soil water potential (Ψ_{soil}) gradients. When atmospheric demand decreases after dark and plant water potential rises, Ψ_{soil} gradients become the dominant gradient for water movement in root systems. Hydraulic redistribution can occur in any direction in the soil profile if there is a Ψ_{soil} gradient (Burgess et al. 2001; Hultine et al. 2004), but the classic example is “hydraulic lift” where deep rooted plants lift water from moist deep soil layers to dry shallow soil layers (Richards and Caldwell 1987). Hydraulic lift can increase the 24-h integrated efficiency of sparse deep roots, thus benefiting plant water and carbon acquisition (Caldwell and Richards 1989). Hydraulic lift has also been widely hypothesized to be a mechanism allowing plants to maintain nutrient acquisition as shallow soil layers dry. The magnitude of hydraulic lift (i.e. diel range in Ψ_{soil}) may directly affect multiple plant and soil processes including root longevity, nutrient uptake in drying soil, rhizosphere microbial and mycorrhizal fungal activity, and nutrient cycling (Richards and Caldwell 1987; Matzner and Richards 1996; Caldwell et al. 1998; Horton and Hart 1998; Querejeta et al. 2003; Domec et al. 2004; Huxman et al. 2004; Warren et al. 2007; Bauerle et al. 2008). The magnitude of hydraulic lift may also affect nutrient uptake on a shorter time scale because the local increases in soil moisture can increase the availability of N in soil solution and increase both soil hydraulic conductivity and effective N diffusivity through the soil to the roots. We investigated the hypothesis that the magnitude of hydraulic lift was related to the short-term ability of a cold desert shrub, *Sarcobatus vermiculatus* (Hook.)

Torrey, to acquire NO_3^- from dry soil layers during the summer growing season.

Sarcobatus vermiculatus is known to exhibit both hydraulic lift and nighttime transpiration in the field (Donovan et al. 2003; Snyder et al. 2003) and grows in nutrient-limited environments. Nighttime transpiration has been proposed as a mechanism for increasing nutrient acquisition by increasing the mass flow delivery of nutrients to the root surface at night (Caird et al. 2007; Scholz et al. 2007). However, in this experiment, we focused on nutrient uptake from shallow soil layers with roots known to exhibit hydraulic lift and thus water was released from some root segments at night. We suppressed nighttime transpiration with the expectation that it would increase the amount of water efflux at night, i.e. the magnitude of hydraulic lift, and thus increase the acquisition of ^{15}N label by those shallow roots during the following day. This expectation was based on past experiments demonstrating that increasing nighttime transpiration reduces the magnitude of hydraulic lift (Caldwell and Richards 1989) and that suppressing nighttime transpiration eliminates one pathway for plant water loss and should increase the alternate pathway of water loss to shallow soils, i.e. hydraulic lift (Donovan et al. 2003). Additionally, the suppression of nighttime transpiration has been shown to increase the magnitude of hydraulic lift for *Artemisia tridentata* and *Helianthus anomalous* under controlled greenhouse conditions (Howard and Donovan, unpublished).

In this field experiment, we supplied ten *Sarcobatus vermiculatus* plants that differed in the magnitude of hydraulic lift with a ^{15}N tracer near shallow roots exhibiting hydraulic lift. Half of the plants were also placed in large humidified tents (i.e. “bagged”), which suppressed nighttime transpiration and were expected to have greater magnitudes of hydraulic lift. We hypothesized that plants with a greater magnitude of hydraulic lift, either inherently or enhanced by suppressing nighttime transpiration, should acquire more $^{15}\text{NO}_3^-$.

Methods

Study site, irrigation treatments and Ψ_{soil} measurements

This research was conducted in July 2001 at the Mono Basin Ecosystem Research Site (MBERS),

California, USA, located at the western edge of the Great Basin biogeographic province (38°5' N, 118°58' W; 1,958 m elev.). Climate at the field site is arid; mean annual precipitation is 160 mm with more than 80% of the precipitation arriving, mainly as snow, between October and May (Snyder et al. 2004). Large *S. vermiculatus* (Hook.) Torrey shrubs (1.34±0.07 m height, mean±1 SE) were selected at the “Diverse Dunes” complex where previous studies on these same shrub populations have described seasonal plant water relations and mineral nutrition (Donovan et al. 1997, 2003). The sandy soils of the dune complex are nutrient poor with water extractable P in the 0–25 cm soil layer averaging 4 mg kg⁻¹ (Donovan et al. 1997). Through the season, KCl extractable NO₃⁻ averages 1.7 mg kg⁻¹ while extractable NH₄⁺ averages 0.7 mg kg⁻¹ (James and Richards 2005).

The present ¹⁵N acquisition study in July 2001 made use of ten similar-sized *S. vermiculatus* shrubs from a larger experiment initiated in 2000 (see Donovan et al. 2003 for details). The shrubs were randomly selected from the natural rainfall (no irrigation, NA) and deep irrigation (DP) treatments in the previous study. For the DP treatment shrubs, pressure compensating drippers delivered irrigation water to a depth of 1.1 m through PVC tubing starting in April 2000. Although the DP treatment was designed to increase the Ψ_{soil} gradient driving hydraulic lift and thus increase the magnitude of hydraulic lift, the shrubs in both treatments had similar predawn water potentials and exhibited similar magnitude hydraulic lift from June to September 2000. Thus, shrubs from these two previous treatments are not differentiated in this study. Ten shrubs were selected to encompass the range of hydraulic lift magnitudes present in the field. For each shrub, the magnitude of hydraulic lift was determined as the diel fluctuation of Ψ_{soil} for each day (i.e. difference between maximum and minimum Ψ_{soil} of the same 24-h period). Soil Ψ was measured with individually calibrated screen-cage thermocouple psychrometers (Series 74, Merrill Specialty Equipment, Logan, Utah, USA) buried at 0.3 m depth. Psychrometer output was logged hourly (CR7, Campbell Scientific Inc., Logan, Utah, USA) and Ψ_{soil} values were calculated following Brown and Bartos (1982), including correction for temperature and zero offset. Readings with zero offsets >5 or <-5 μV were discarded, however most offsets were between 2 and -2 μV , a range that allows accurate Ψ_{soil} measurement (Brown and Bartos 1982).

Injection of the ¹⁵N label occurred on July 15 (see below for methods), for each shrub. The magnitude of lift was averaged for two time periods: 4 days that preceded the ¹⁵N injection (July 8–11) and 4 days after injection (July 16–19).

Shrubs were paired by lift magnitude prior to ¹⁵N injection and one shrub from each pair was randomly selected to receive a “bagging” treatment ($n=5$ pairs). Bagging treatments minimized nighttime transpiration and were expected to increase the magnitude of hydraulic lift. Bagged plant crowns were covered with a PVC frame which held a wetted fabric tarp for humidification inside the bag and supported the polyethylene sheets forming the bag (or tent). Bags were installed at dusk just before darkness, sealed around the margin with sand and removed at sunrise. Plants were bagged each night for the first three nights after ¹⁵N injections (see below).

Measurements of nighttime leaf gas exchange (LI-6400, LiCor Inc., Lincoln, Nebraska, USA) and shoot water potential (Model 1000 pressure chamber, PMS Instrument Co., Albany, Oregon, USA) were made on the first night of bagging on shrubs adjacent to and in the same irrigation treatments as the 10 focal shrubs (see Donovan et al. 2003 for method details).

In the year prior to this ¹⁵N experiment, minimizing nighttime transpiration with “bagging” increased predawn plant water potentials by approximately 0.6 MPa over unbagged control shrubs (measured with Model 1000 pressure chamber, PMS Instrument Co., Albany, Oregon, USA). Nighttime stomatal conductance in the unbagged shrubs ranged from 0.03 to 0.10 mol m⁻² s⁻¹ and transpiration under ambient conditions ranged from 0.47 to 0.87 mmol m⁻² s⁻¹ (measured with LI-6400, LiCor Inc., Lincoln, Nebraska, USA) (Donovan et al. 2003). On the first night of bagging in this ¹⁵N experiment nighttime, leaf gas exchange and shoot water potential were again measured on shrubs adjacent to and in the same irrigation treatments as the 10 focal shrubs (see Donovan et al. 2003 for method details). Nighttime stomatal conductance of unbagged control shrubs was 0.028±0.004 mol m⁻² s⁻¹ and transpiration was 0.3±0.05 mmol m⁻² s⁻¹ (means±1 SE, $n=14$). Additionally, stem predawn water potentials of bagged shrubs and adjacent unbagged control shrubs were -1.4±0.16 MPa and -1.9±0.1, respectively. These data indicate that during the previous growing season and during this study, the experimental shrubs had open stomata at night and that bagging

effectively suppressed nighttime transpiration resulting in increased leaf water potential.

Soil ^{15}N labeling and plant ^{15}N acquisition

The effect of hydraulic lift on plant N acquisition was evaluated by quantifying N uptake from soil microsites labeled with ^{15}N . The ^{15}N label was applied at dusk on 15 July 2001. For each experimental shrub, ^{15}N was applied by injecting 25 ml of 50 mM K^{15}NO_3 (98 at.% ^{15}N) in each of five microsites. The first microsite was centered over the buried psychrometer near the canopy drip line and the other four microsites were distributed 15 and 30 cm from the psychrometer in two directions roughly parallel to the canopy drip line. A syringe and large metal needle, with a sealed tip and four lateral holes, were used to inject the solution. The sealed tip of the needle was inserted 30 cm into the soil and slowly pulled up 10 cm through the 20–30 cm soil profile as the ^{15}N solution dispersed horizontally through the four holes drilled above the sealed tip. By applying a small amount of highly enriched N in our microsites, we were able to trace plant NO_3^- acquisition without significantly increasing soil inorganic N pools or soil water content.

We quantified ^{15}N acquisition by the experimental plants by harvesting randomly selected leaves from around the plant canopy (approximately 1.5 g dry weight) before application of the label and 1, 2, 3, and 9 days following label application. We quantified changes in leaf ^{15}N pools using a ^{15}N mass balance equation (Nadelhoffer and Fry 1994) as:

$$^{15}\text{N}_{\text{rec}} = m_{\text{pool}} \frac{(\text{at.}\%^{15}\text{N}_{\text{pool}} - \text{at.}\%^{15}\text{N}_{\text{ref}})}{(\text{at.}\%^{15}\text{N}_{\text{tracer}} - \text{at.}\%^{15}\text{N}_{\text{ref}})}$$

where $^{15}\text{N}_{\text{rec}}$ is the mass of ^{15}N tracer recovered in the labeled pool ($\mu\text{g plant}^{-1}$); m_{pool} is the N content of the labeled leaf pool (μg); $\text{at.}\%^{15}\text{N}_{\text{pool}}$, $\text{at.}\%^{15}\text{N}_{\text{ref}}$, $\text{at.}\%^{15}\text{N}_{\text{tracer}}$ are the atom percent of the labeled N leaf pool, non-labeled reference leaf pool, and tracer, respectively. All leaf samples were triple rinsed with deionized water, oven-dried at 65°C to a constant mass and finely ground. Tissue N concentration and ^{15}N enrichment were measured by continuous flow direct combustion and mass spectrometry at the University of California Davis Stable Isotope Facility (Europa Integra, London; [http://stableisotopefacility.](http://stableisotopefacility.ucdavis.edu)

[ucdavis.edu](http://stableisotopefacility.ucdavis.edu)) and the University of Georgia, Institute of Ecology Stable Isotope Laboratory (<http://www.uga.edu/sisbl/>). Leaf ^{15}N pools quantified in leaves were scaled to the entire plant canopy following the methods of (Andrew et al. 1979). Scaling methods included harvesting a representative branch unit from each of the ten shrubs and then visually estimating, with two observers, the number of branch units with similar leaf area contained within a shrub. Leaves were removed from the representative branch units and dried and weighed. Total leaf biomass of each shrub was obtained by multiplying the leaf biomass of the branch unit by the number of branch units in each shrub. This was done to account for differences in absolute shrub size and to estimate the total leaf N pools.

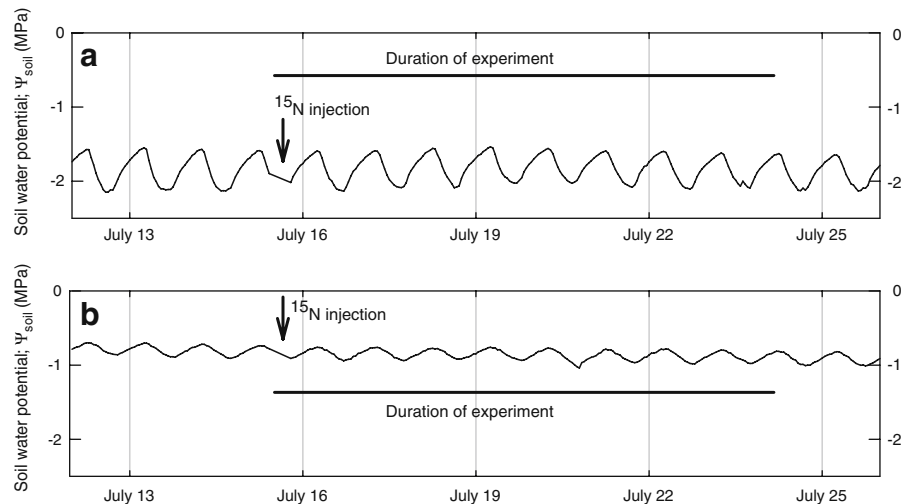
Statistical methods

To determine if bagging and time (prior to injection versus after injection) altered the magnitude of hydraulic lift we used repeated measures ANOVA (JMP-SAS Institute). This was necessary as a first step to determine whether hydraulic lift was affected by either the injection of a small amount of water (which would decrease lift), or the bagging treatment (which would increase lift).

To determine if background (i.e. average) Ψ_{soil} interacted with the magnitude of lift or with the final amount of ^{15}N acquired, a simple linear regression between lift magnitude and absolute Ψ_{soil} was calculated. A multiple linear regression was performed with final ^{15}N acquisition as the dependent variable and lift magnitude and average Ψ_{soil} as multiple continuous independent variables (JMP-SAS Institute).

Next we explored several other models for leaf ^{15}N acquisition ($\mu\text{g plant}^{-1}$). The full model examined the main and interactive effects of bagging treatment and time (days since injection) on leaf ^{15}N uptake, with the magnitude of lift after injection as a covariate, using a repeated measures mixed model (SAS Institute 2003). This model was then limited to only two-way interactions. The covariate did not significantly explain any of the variation; consequently, the magnitude of lift was not used in the simplified model. The simplified model examined the effects of bagging treatment and time on leaf ^{15}N uptake. Treatment comparisons were made at each time point using the slice option to test the hypotheses that

Fig. 1 Representative plots of hourly measurements of soil water potential (Ψ_{soil}) from two *Sarcobatus vermiculatus* shrubs measured in the current study. **a** An example of large magnitude hydraulic lift and **b** an example of small magnitude hydraulic lift. Arrows indicate the day when the ^{15}N label was injected and straight lines indicate the time period of the experiment



decreased nighttime transpiration (i.e. bagging treatment) affected ^{15}N uptake. The error variances of the simplified model were plotted and found to meet assumptions of repeated measures ANOVA. Therefore, raw data values are summarized and means and standard errors are presented in the text and figures.

Results

As expected, there was a substantial range in magnitude of hydraulic lift among the ten study shrubs (Figs. 1 and 2) (see also Donovan et al. 2003). Two representative study shrubs, one with small magnitude hydraulic lift and one with large magnitude hydraulic lift are presented for reference (Fig. 1). The range of the magnitude of lift (diel variation in Ψ_{soil}) before ^{15}N injection was 0.08–0.56 MPa for the five bagged shrubs and 0.15–0.31 MPa for the five unbagged shrubs. After injection the ranges were 0.08–0.52 and 0.03–0.25 MPa for bagged and unbagged shrubs, respectively (Fig. 2). The magnitude of lift prior to injection of label was not different from the magnitude of lift after injection based on repeated measures ANOVA, which indicated no effect of bagging ($P=0.34$), time ($P=0.81$) or the interaction of time and bagging ($P=0.77$) on hydraulic lift. One or two of the psychrometers showed a damping after the injection with the label, indicating that the small amount of water was actually injected very close to the psychrometer, but the overall effect was not significant. Unexpectedly,

our bagging treatment did not appear to increase lift. If the bagging treatment did increase lift it was either too small of a change to be detected by the psychrometers or in an area of the rooting volume not measured by the psychrometers.

Linear regression indicated that there was no significant relationship between average Ψ_{soil} and the magnitude of lift ($P=0.61$, data not shown). Additionally, multiple regression showed that there was no significant relationship between final ^{15}N capture and average Ψ_{soil} or the magnitude of lift ($P=0.60$, data not shown).

To understand the effects of bagging, time, and the magnitude of lift on leaf ^{15}N capture, we tried several

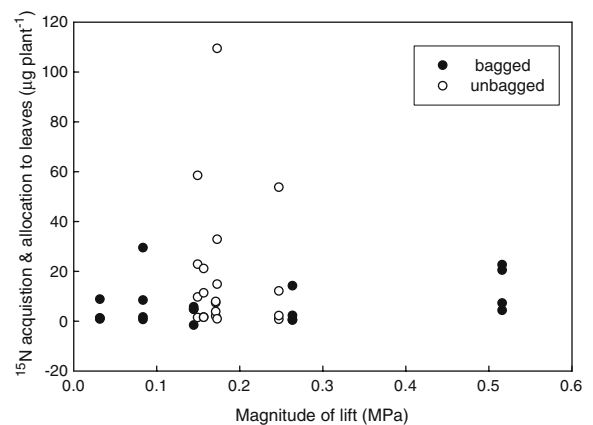


Fig. 2 There was no significant effect of the magnitude of hydraulic lift after injection on ^{15}N acquisition and allocation to leaves ($\mu\text{g plant}^{-1}$) of *Sarcobatus vermiculatus*. Bagged (closed circles) and unbagged plants (open circles) are shown

repeated measures models using the magnitude of lift as a covariate. The magnitude of lift and its interaction with the other factors did not significantly explain the variation in leaf ^{15}N uptake ($P>0.54$). Due to small sample size and multiple effects, inclusion of this covariate reduced the explanatory power of the other variables. Therefore, we also used a simplified model with only the effects of bagging and time on leaf ^{15}N uptake.

Plant ^{15}N increased over the 9 days after injection and this was a highly significant effect ($P<0.01$; Fig. 3). The main effect of bagging was also likely significant ($P=0.07$) considering the small leaf sample sizes and high variance among leaves within the canopy with non-bagged plants having much greater uptake of ^{15}N than bagged treatment plants (Fig. 3). Slice effects analysis indicated that 3 days after injection of the label, unbagged plants had 2.8-fold greater ^{15}N acquisition than bagged plants ($P=0.09$; Fig. 3). The final ^{15}N accumulation, 9 days after injection, was also greater, 3.1-fold, in unbagged than in bagged plants ($P=0.09$). These data indicate that nighttime transpiration, which continued for each of the three nights after ^{15}N injection in unbagged but not in bagged plants, may play a role in nutrient acquisition.

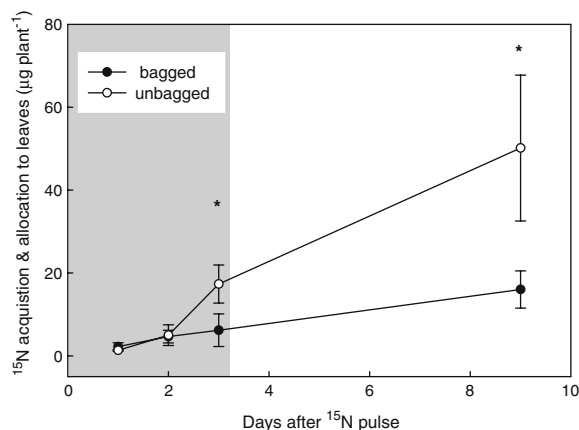


Fig. 3 Mean (± 1 SE; $n=5$) ^{15}N acquisition and allocation to leaves ($\mu\text{g plant}^{-1}$) through time for both bagged (closed circles) and unbagged plants (open circles). Shaded area indicates when daytime sampling was preceded by nighttime bagging. The main effect of bagging was marginally significant ($P=0.07$) and differences at 3 and 9 days after injection, as determined with the slice option within a repeated measures ANOVA (SAS Institute 2003), were also marginally significant (* $P=0.09$ for both days)

Discussion

This experiment demonstrated that the range of hydraulic lift assessed in this study did not affect ^{15}N uptake, but we were able to detect ^{15}N uptake in large shrubs over a short time period and with very localized injections of ^{15}N into dry soils. Although there is a great deal of speculation about the adaptive significance of hydraulic lift, this is difficult to test because it is not easy to suppress hydraulic lift without eliminating roots and therefore have “true” controls in field settings. However, to our knowledge this is the first experiment to attempt to test, under field conditions, if short-term N capture is enhanced by hydraulic lift. We did not find any effect. It is plausible that the range of lift was not broad enough to elucidate the effects of hydraulic lift on plant N uptake. The variation in magnitude of hydraulic lift in this study (0.03–0.56 MPa) is consistent with that reported for these shrubs for June to September of the previous growing season and is thus representative of this species (Donovan et al. 2003). Additionally, it is possible that the timing of this experiment did not coincide with the period of maximum N demand for this species. In a separate study at the same research area, smaller *S. vermiculatus* shrubs were found to have greatest uptake of ^{15}N in early spring (James and Richards 2005). In any case, the small hydraulic lift-induced increases in shallow soil moisture did not increase short-term N uptake in this sandy dune system.

Although the effect of suppressing nighttime transpiration was only marginally significant, there appears to be a consistent pattern contrary to our expectation: plants with suppressed nighttime transpiration had decreased ^{15}N uptake. Several recent studies have produced mixed results as to whether nutrient limitations result in increased nighttime stomatal conductance and transpiration (see review by Caird et al. 2007, and Howard and Donovan 2007; Scholz et al. 2007). However, it is plausible that plants may not regulate nighttime transpiration in response to nutrient status, but that improved nutrient acquisition is a passive result of nighttime transpiration (Caird et al. 2007). More studies are needed to determine the potential effect of nighttime transpiration on plant nutrient acquisition, as suggested by our data.

We need to consider why the plants that remained unbagged at night had apparently higher ^{15}N acqui-

sition even though they continued to exhibit hydraulic lift and thus had a net flux of water *away* from roots at night at the depth where the ^{15}N tracer was injected. This means that the decrease in uptake of $^{15}\text{NO}_3^-$ associated with nighttime bagging is not likely attributable to a net decrease in transpiration-driven mass flow delivery of the label to roots, but to some other effect. One possibility is that bagging affected the nitrate diffusion gradient around the roots and/or the effective diffusivity of nitrate, which could outweigh the small amount of mass flow away from active roots (Tinker and Nye 2000). A second possibility may involve heterogeneity in soil moisture and root processes in the shallow soils. The roots affecting the small soil volume measured by the psychrometer may have been releasing water at night via hydraulic lift, while other shallow roots or root segments were not losing water but continued to absorb the ^{15}N label. Apoplastic gaps near root tips and at points of lateral root emergence are locations where hydraulic lift water efflux would be more pronounced, while root segments without such gaps could have lower water efflux or even localized water influx in response to the nighttime transpiration and thus have the potential for nutrient acquisition (Steudle 1994; Matzner and Richards 1996; Caldwell et al. 1998). The increased acquisition of ^{15}N could then be due to a greater total uptake of water.

A third alternative is that bagging had effects on other variables such as daytime gas exchange and transpiration that indirectly reduced daytime ^{15}N acquisition. Bagging increases predawn leaf water potentials (Donovan et al. 2001, 2003), but small gains in leaf water status may have been offset by other factors that influence daytime gas exchange. For example the bagging obviously increased relatively humidity and decreased the leaf-to-air vapor pressure deficit at night, since this is how we suppressed nighttime transpiration. However, bagging may have also increased nighttime air temperature and CO_2 concentration around the canopy, possibly decreasing stomatal conductance and transpiration after plants were unbagged at sunup. It has been suggested that nighttime transpiration may be a mechanism that enhances gas exchange in the early morning hours because plants already have their stomata open (Dawson et al. 2007). Additionally, high external CO_2 at night may lead to excessive CO_2 buildup in leaves, which could decrease carbo-

hydrate export potentially decreasing the regeneration of RuBisCo and inhibiting photosynthesis the next day (Marks and Lechowicz 2007). Thus, although unlikely, if nighttime bagging reduced daytime gas exchange, it could explain why bagged plants had less ^{15}N acquisition.

Finally, bagging may have had no direct effect on ^{15}N acquisition, but may have indirectly affected where the ^{15}N was stored within the plant. Nitrate is readily mobile in the xylem but can be stored in vacuoles of cells in many organs. We did not quantify N stored in roots or stems in this study. Nighttime transpiration has been found to increase the amount of predawn disequilibrium in this species (Donovan et al. 2003) creating a stronger water potential gradient from soil to leaves, and this could result in more N being transported immediately to leaves. In contrast, the gradient in bagged plants would be less to leaves and relatively more to the roots perhaps resulting in more N being retained in roots.

Questions remain about how nighttime transpiration can increase N acquisition or affect allocation of captured N, as well as about the interplay between hydraulic lift and nighttime transpiration. In the current study variation in the magnitude of lift was not related to the amount of ^{15}N acquired in the short term, but reduction of nighttime transpiration decreased the amount of ^{15}N captured and allocated to leaves. These data suggest that there may be a more complex relationship between plant water use and nutrient acquisition in this nutrient- and water-limited environment than previously recognized. As both hydraulic lift and nighttime transpiration are widespread in plants, similar interactions may be occurring widely for many plant species.

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